ON THE PAUCITY OF INTERTIDAL BARNACLES IN THE TROPICAL WESTERN PACIFIC

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(Plates 20 and 21)

Barnacles or cirripedes are familiar organisms to nearly all who frequent the shores of temperate waters. So abundant are they that one tends to consider them common intertidal animals. In the preface to his monograph on the American sessile barnacles, H. A. Pilsbry (1916) speaks of them as one of the dominant groups of littoral animals. Indeed, it has been said that the present period may go down in the fossil record as the age of barnacles. This may be true in temperate waters but it is certainly not true of the tropics.

The California coast supports about six genera and twenty-five or so species of barnacles. Only a few of these species account for the abundance of intertidal individuals. On the other hand, nearly 250 species of barnacles are recorded from the Indo-Pacific. At least half this number are littoral and intertidal forms. However, although there are many different kinds, actual numbers of individuals are astonishingly small. This was perhaps first recognized by Darwin (1851-54) who pointed out that, for some reason, coral reefs are apparently unfavorable for barnacles. It is the purpose of this note to present some evidence as to why this should be the case for intertidal forms.

The principal collections and observations made in conjunction with this study were at Truk in the Caroline Islands. Supplementary work was done at Majuro in the Marshall Islands and at Guam in the Mariana Islands. Evidence contributed by others from different localities is cited in the text. In nearly all cases, corals or the littoral limestones produced by them are prominent features of the situations under consideration.

The physical conditions under which reef-building corals flourish are well known. In general, they are restricted to the photic zone where surface waters are 21°C or warmer and they require clean, well oxygenated waters. Silty, poorly oxygenated, or diluted sea water is unfavorable for vigorous growth. In contrast, intertidal barnacles abound in cool temperate seas. Certain species flourish in turbid, and even stagnant, conditions, and some of the most luxuriant barnacle populations occur in estuaries, where seasonal dilution, variable temperatures, and turbidity are common.

We know under what conditions corals and barnacles grow abundantly, but there is little evidence as to why conditions other than these should be unfavorable. It is believed that physical conditions of the environment limit coral distribution, in that the number of species and the number of individuals or colonies become less as one moves away from tropical conditions. The number of barnacle species undergoes the same sort of decline as one moves away from the tropics. However, a paradox exists in that, although there are fewer temperate barnacle species, the relative number of individuals is great and they progress from an inconspicuous tropical element to one of the dominant temperate littoral forms. Thus, it would appear that barnacles are best adapted to temperate waters. It is not the exceedingly greater variety of barnacle species that exist in the tropics that encourages me to pursue this subject, but rather it is the fact that barnacles were occasionally found in great profusion in certain natural and artificial situations in tropical waters. It is hoped that a consideration of these special situations and conditions will demonstrate that primarily biotic factors account for the relative paucity of intertidal barnacles in the tropical Pacific.

A clue to the nature of what limits barnacle abundance can be gained by a brief consideration of the types of habitats in which they occur. In general, there are three basic ones: some barnacles being found in or on fixed substrates, in or on other animals, and on inanimate objects floating in the sea. Although we are primarily concerned with the first of these, the others have indirect bearing on the overall problem.

In a relatively short time nearly any object that floats in the sea becomes covered with pedunculate barnacles. Specimens of Lepas spp. and Conchoderma virgatum were found washed up on reefs and beaches on pieces of pumice, cuttle bone, Nautilus shell, feathers, segments of Pandanus fruit, coconuts, and on glass fishing floats. The regular occurrence and abundance of these forms would indicate that although ocean and lagoon waters are highly transparent, they are not sterile but contain quantities of "barnacle forage". The habitat of the floating forms differs conspicuously from that of the littoral groups in that they are never associated with corals and are never uncovered by the tides.

In the temperate zone, one commonly finds sessile barnacles on littoral gastropod and bivalve mollusk shells and on large decapod crustacea. Generally, these barnacles are not particularly modified or specialized forms, but simply occur on the hard parts of other organisms occupying essentially the same level in the littoral zone. In cataloguing nearly 140 species of shelled mollusks in the tropics and handling probably ten times this number of individuals, not a single epizoic barnacle was found. Decapod crustacea, on the other hand, are often infected with specialized pedunculate barnacles. Members of the genus Octolasmis were taken in the branchial chambers of the Mangrove crab, Scylla serrata (Forskal) (1), the Slipper lobsters, Parabaccus antarcticus (Lund) (2), and Scyllarides squamosus (Milne-Edwards) (3). Another species of Octolasmis was found on the mouth parts of Scyllarides and another pedunculate, Heteralepas palinuri Barnard(1924), was taken from the mouth parts of the Spiny lobster, Panulirus penicillatus (Oliver) (2). All of these species have undergone a considerable degree of disarmament as compared with their free living counterparts, and this is clearly in response to the degree of protection afforded by their host. Octolasmis is of special interest for it occurs in such numbers as to suggest that physical conditions favor its existence; a factor contributing to its survival being the protection received from its host.

Barnacles found with corals are often specialized burrowing forms. One of the commonest coral burrowers is the fairly large pedunculate, Lithotrya. Another group, the order Acrothoracica, is composed entirely of burrowing forms, many of which inhabit corals. Among the sessile or acorn barnacles, Pyrgoma and Creusia burrow, or are buried, in living corals, and species of Balanus may occur with corals in situations where they receive mechanical protection from bends and folds in the coral skeletons. Since corals usually do not survive exposure to air during low tides, these barnacles are subtidal forms. They are rarely found with their shells fully exposed. The striking feature about the group is the protection it derives from corals and coral remains.

The pedunculate Ibla cumingi Darwin and the sessile genera Balanus, Chthamalus, and Tetraclita have true intertidal forms. These were never found on mollusk or crustacean hard parts. They tended to occur sparsely in intersticies in or between and under rocks. Chthamalus occurred on high beach rock (1,2,4) covered only during high tides. Chthamalus was also found in fair numbers in brackish water areas and Mangrove swamps. Such areas are usually muddy and the barnacles grow on sticks, Mangrove prop-roots, and other solid substrates (1).

Other high intertidal areas were not found to support barnacles excepting in areas protected from wave action or where volcanic rock occurs. Coral limestone, unlike volcanic rock, is rather light in weight and smaller boulders are rolled around by wave action. This scouring probably accounts for the lack of barnacles along rubble ramparts. In general, then, the great reef-flat, the rubble rampart along reef islets, tide pools and the like, the entire intertidal zone between the lowest and highest reaches of the tides, is markedly deficient in numbers of barnacles. So sparse are they that they can be considered as relatively rare, inconspicuous intertidal organisms. What stark contrast to the shores of temperate waters!

In the subtidal, where corals abound, it is possible that the corals themselves or something about the coral association limits the numbers of barnacles. Competition between corals and barnacles for food would appear not to be a significant factor, for barnacles do occur with corals. In general, subtidal forms either exist under varying degrees of mechanical protection or are removed from the reef-building coral association. Yet it is apparently not the living corals that are entirely responsible for the lack of abundance, for in the intertidal, which is generally destitute of living corals, barnacles do not flourish either. Something besides corals, something outside of the strict coral association must be unfavorable for intertidal forms.

The herbivorous fish that forage over the reef during high tides are of a very different sort than those that feed on sea weeds along our coasts. In contrast, they are provided with a variety of incisor-like teeth with which they rasp away at the limestone reef for the microscopic algae growing on its surface. In their rasping they remove substantial amounts of substrate. It would appear that their raspings may be responsible for an appreciable amount of erosion of limestone reefs. These fish are, in their manner of feeding, predators on such fixed organisms as barnacles, especially on freshly settled larval stages and young individuals. The Chaetodontidae (Plate 21, Figure 3c), Acanthuridae (Plate 21, Figure 3b), Labriidae (Plate 21, Figure 4b), Balistidae (Plate 21, Figure 4c), Diodontidae, and Tetradontidae represent some of the groups that have modified dentition enabling them to gnaw or rasp corals and limestones. Observations were made on various members of these groups. The acanthurids were perhaps the most abundant raspers this author noted on reef-flats at Truk, Guam, and Majuro. While lying face down in shallow water during rising tides and looking beneath the surface along the reef, one may see the dark shapes of these fish gradually moving shoreward. Their progress is slow as they bob head downward over the limestone surface. Assumedly they are nibbling and rasping at the substrate, as their gut contents were found to be white and gritty with limestone or fine coral sand.

It has already been mentioned that subtidal littoral barnacles are generally modified forms that are mechanically protected in some way. That this protection is from predators is problematical. That it is from rasping fish is perhaps too strong a suggestion. However, an observation made in a special situation tends to place some predators associated with corals under suspicion. In the Truk lagoon there are several large channel markers that were put in by the Japanese prior to or during World War II. These buoys are exposed on all sides by open water and are slowly sinking due to the accumulated weight of corals growing on their submerged parts. Samples of coral broken from one of these buoys were heavily encrusted by the sessile barnacle Tetraclita (Tesseropora) sp. (Plate 20, Figure 1). The unique feature about the buoys, aside from the profusion of exposed barnacles growing with the corals, was the apparent absence of reef fishes which normally inhabit coral reefs. It is possible that fish had not become established during the period the buoys were in the water or that there was not enough coral to support them, but it seems more likely that a lack of shelter from piscivorous forms accounts for their absence.

A somewhat analogous situation exists in the intertidal. On Heron Island, Australia, it has been observed (Endean, et al., 1956) that there is a general paucity of intertidal barnacles on high beach rock. However, barnacles were found around the higher portions of "nigger heads" or storm rocks out on the reef crest. It has been suggested (5) that, as the tide comes in, predatory fish drive the raspers into hiding or up into relatively shallow water. This leaves the higher reaches of the storm rocks free of rasping fishes and this is believed to account for the barnacles found there.

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EXPLANATION OF PLATES

Plate 20

Figure 1: Tetraclita (Tesseropora) sp. on the coral cf. Pocillopora sp. taken from a buoy in Moen-Dublon Channel, Truk, Caroline Islands. Note the crowded exposed barnacles encrusted with algae and aborescent bryozoa. X 2. Figure 2: Chthamalus stellatus (Poli) on high intertidal beach rock (limestone) from Nimitz Beach, Guam, Mariana Islands. Note the uniform systematic pattern of tooth marks covering the surface of the rock. X 2.25.

Plate 21

Figure 3a: Same rock and barnacles as shown in Figure 2, enlarged. Note the parallel line of tooth marks indicated by the arrow. These were made by a single fish, probably an acanthurid, rasping, bite after bite, across the face of the rock. These marks are conspicuous because they are more recent than the surrounding marks and algae have not grown in to restore the natural color. The small barnacles (near center) were narrowly missed by the teeth of the fish that made these marks. X 7. Figure 3b*: Profile of the jaws and teeth of Acanthurus. Figure 3c*: Profile of the jaws and teeth of Chaetodon. Figure 4a: Same rock as shown in Figure 2, enlarged. Note the large tooth marks that have resulted from a single rasping bite of fish on the projecting edge of the rock. The fish was probably a balistid or wrass. Marks of this size were infrequently encountered on the rocks of Nimitz Beach. However, rock from Truk, Kapingamarangi, and Majuro was commonly and heavily scarred in this way. X 6. Figure 4b*: Profile of the jaws and teeth of a labriid. Figure 4c*: Profile of the jaws and teeth of Balistes.

* Not to scale

Figure 1

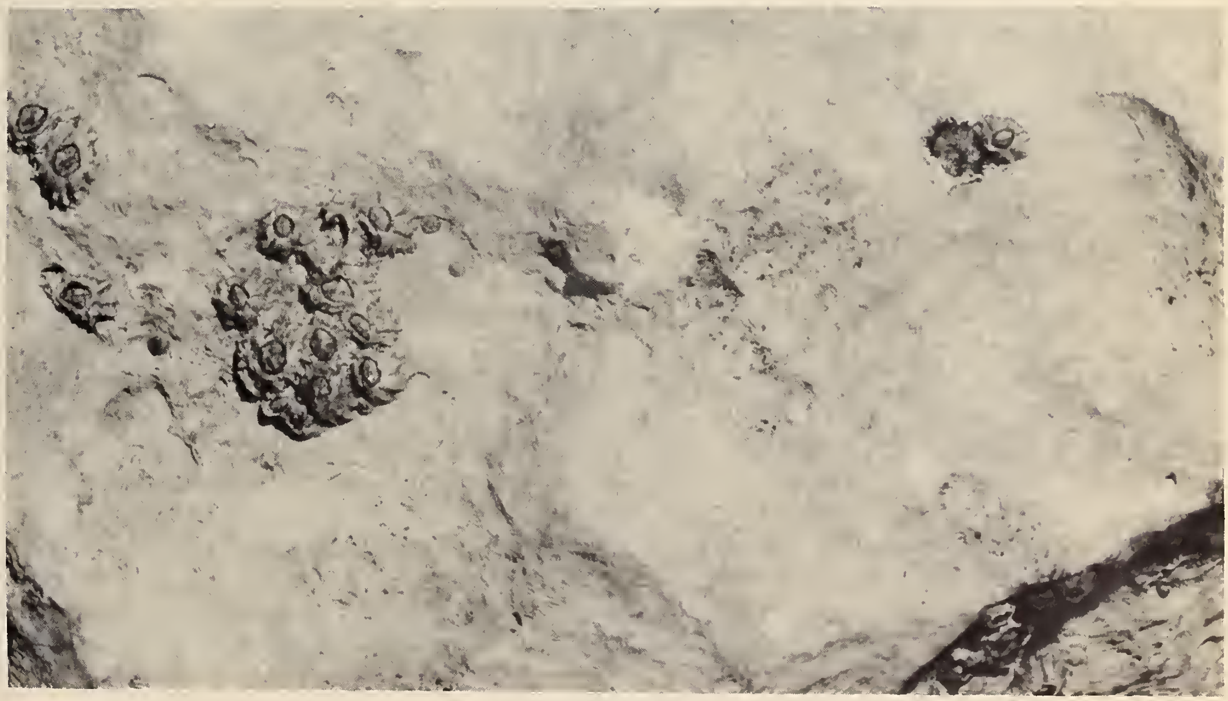

Figure 2